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Lion (*Panthera leo*) population dynamics: do nomadic males matter?

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Lay Summary

Males matter, especially in species like lions (*Panthera leo*). We report on the analysis of individual-based data of male lions in Serengeti National Park. We observed a significant decrease in male immigration to our study area from surrounding areas, which resulted in lowered levels of male replacement, reduced infanticide, and greater cub survival. The protected population might compensate for rising lion mortalities in surrounding areas, but as anthropogenic pressures intensify, compensatory mechanisms may become overwhelmed.

Abstract

Key population processes are sometimes driven by male dynamics, but these drivers are often overlooked because of the scale over which they operate. Lions (*Panthera leo*) provide an ideal case study for investigating factors governing male dynamics and their influence on population sustainability. Lions display sexually selected infanticide, and resident males must defend their offspring from nomads that may have dispersed over long distances; factors affecting male-male competition over large spatial scales can have population wide consequences. We report here on the first systematic analysis of long-term individual-based data of male lions in the Serengeti National Park, Tanzania. From 1974-2012, we observed 471 coalitions (796 males) in our study area. We investigate factors affecting male immigration and the impacts on the resident population. The yearly number of nomadic males entering the study population affected cub survival and mating access. Success rates of nomadic males gaining tenure with a pride increased with age and coalition size. We observed a significant decline in male immigration, which resulted

in lowered levels of male replacement in the study population, reduced infanticide, and greater cub survival. The decline in incoming males likely resulted from increased anthropogenic pressures in surrounding areas. Conversely, the core study population was largely buffered from anthropogenic threats and likely served as a source to neighboring sinks. Reduced infanticide in the core population might have compensated for rising lion mortalities in surrounding areas, but as human-wildlife conflicts intensify with the rapidly growing human population, compensatory mechanisms may become overwhelmed.

Introduction

Sustainable wildlife management is becoming increasingly difficult in the face of expanding human populations, habitat fragmentation, and climate change (Delsink et al., 2013; Pitman et al., 2015; Treves and Karanth, 2003). For large mammals, population measures are essential for conservation planning and management (e.g. estimates of population decline are integral to IUCN-status criteria and quota-setting for CITES exports). Mitigating population declines is especially challenging for large mammals, where demographic consequences may only be detectable at large spatial or temporal scales. Mitigation planning requires a solid mechanistic understanding of population drivers, such as compensatory effects (Poysa, 2004), ecological traps (Pitman et al., 2015), and edge effects (Balme et al., 2010). Demographic studies often ignore males (Borrego et al., 2008; Lindstrom and Kokko, 1998; Moller, 2003; Rankin and Kokko, 2007), even though male dynamics often drive population processes through density-dependent effects, e.g. resource limitation, disease transmission, sperm limitation, and

infanticide (Andreassen and Gundersen, 2006; Ginsberg and Milner, 1994; Milner et al., 2007; Rankin and Kokko, 2007; Swenson et al., 1997). Males can even regulate populations via dispersal patterns, territorial structure, and reproductive strategies (Elliot et al., 2014b; Milner et al., 2007; Odden et al., 2014), and extreme alterations in male dynamics can lead to rapid population decline (Milner et al., 2007; Whitman et al., 2007). Thus, identifying factors governing male dynamics is essential for mitigating anthropogenic factors that affect population stability or sustainability.

Male mediated effects are particularly consequential in species with sexually selected infanticide (SSI). SSI can occur when nomadic males gain increased mating success by ousting resident males and killing dependent young they did not sire (Ebensperger, 1998; Hrdy, 1974). If nomads replace residents too frequently, the rate of infanticide becomes unsustainable, thereby leading to population decline (Swenson, 2003). Population destabilization is further amplified in these species when males are disproportionately targeted by anthropogenic activities (Packer et al., 2011; Rankin and Kokko, 2007; Whitman et al., 2004; Whitman et al., 2007). For example, trophy hunters often preferentially target males for their large size. The resultant excessive off-take of prime-aged males increases infanticide by nomadic males, and if left unchecked, may result in population collapse (Packer et al., 2011; Whitman et al., 2004; Whitman et al., 2007). Studies investigating male dynamics often focus on the resident segment of the population, ignoring factors affecting nomadic male dynamics. However, in SSI species, nomads likely play a pivotal role in population regulation.

Long-lived and wide roaming, African lions (*Panthera leo*) are an iconic species facing broad population decline, and provide an ideal case study for investigations of male

dynamics and the influence of nomadic males in this context. Lions live in permanent female groupings (prides) that maintain exclusive territories and are temporarily defended by male coalitions (Schaller, 1972); males compete with each other for prides and nomadic coalitions attempt to oust residents (Bygott et al., 1979). Males disperse from their natal pride when they reach maturity or are prematurely ousted by a rival coalition (Bygott et al., 1979; Pusey and Packer, 1987). Nomadic takeovers are the primary driver of natal dispersal, resulting in large variation in dispersal age, with higher mortality among young dispersers (Elliot et al., 2014a), and infanticide by nomads mediates population growth (Andreassen and Gundersen, 2006; Milner et al., 2007; Odden et al., 2014; Pusey and Packer, 1987; Whitman et al., 2004).

Males disperse as a cohort and may spend years in a nomadic phase before gaining residence in a pride (Hanby and Bygott, 1979). Following a pride takeover, newly resident males kill the ousted coalition's cubs, and evict male subadults and non-breeding age female subadults (Bertram, 1975; Packer and Pusey, 1983a, b). Resident males must maintain tenure for about two years so as to rear descendant cubs to independence (Packer and Pusey, 1983a; Whitman et al., 2007). Thus, in species like lions, male dynamics affect mate access, offspring survival, social organization, and ultimately affect population level changes (Spong and Creel, 2004; Spong et al., 2008; Swenson et al., 1997).

The majority of prior demographic research has focused on coalitions resident in breeding prides, but nomadic coalitions represent a potentially powerful disruptive force in populations. We report here on the first systematic analysis of long-term individual-based data of nomadic males in the Serengeti National Park, Tanzania. Lion populations

in Tanzania are at risk from several anthropogenic threats, including trophy hunting, retaliatory killing, poaching, and habitat loss (Kissui, 2008; Packer et al., 2009). Lions in the Greater Serengeti Ecosystem have been exposed to varying degrees of sport hunting and an ever-increasing number of subsistence farmers and livestock herders in the surrounding areas, which has been linked to lion population declines, resulting in varying numbers of nomads entering the long-term Serengeti study area over the past five decades. Thus, our study system provides a natural experiment to test the effects of nomadic males on key population processes: mate access, offspring survival, immigration, and population growth. We investigated the factors affecting the number of nomadic male lions immigrating into the study area, factors predicting nomadic coalitions gaining tenure with a breeding pride, and the effects of nomad dynamics on the resident population. We hypothesized resident-nomad competition and nomad-nomad competition significantly affects nomads' ability to gain tenure and residents' ability to maintain tenure with study prides, respectively. We apply this mechanistic understanding to principles underpinning conservation planning.

Methods

Study area and population

Our study area encompassed 2,000 km^2 of Serengeti National Park (SNP), located within the 25,000 km^2 Serengeti-Mara ecosystem (Fig. 1). The SNP study area consists of two broad habitat types: acacia woodlands and open grasslands. The ecosystem is characterized by distinct wet (November-May) and dry (June-October) seasons, which vary annually according to the strength of the Southern Oscillation Index (SOI) (Sinclair

et al., 2013). SNP is bordered by the Ngorongoro Conservation Area (NCA), Maswa, Grumeti and Ikorongo Game Reserves (GRs), and the Loliondo game controlled area (GCA). Trophy hunting is allowed in the GRs and GCA but not in the NCA and SNP (Packer et al., 2011); pastoralist Maasai live in the NCA and GCA (Fig. 1).

Prides in the SNP were monitored during 1974-2015 (Packer, 1986). From 1974 to 1983 all observations were based on systematic search across the landscape with 1-2 vehicles driving ca. 75 km per day for 5-6 days per week. Beginning in 1984, one female per pride was fitted with a radio collar, and prides were located by radio telemetry at least once every two weeks (VanderWaal et al., 2009). Lions born in the study area were first identified as cubs based on whisker spots; age estimates for immigrants were based on nose coloration, coat condition and tooth wear (Packer and Pusey, 1993; Whitman et al., 2004). Demographic events (births, deaths, coalition takeovers, immigration, and emigration) were based on direct observation. Nomadic males were defined as individuals that had not previously gained tenure with any study pride and were either not born into a study pride or born into a study pride but absent from the study area for a minimum of two years. A nomadic coalition was considered to have gained tenure with a pride following observation with the pride's females on at least three separate occasions, whereupon they were defined as becoming a resident coalition. A nomadic coalition was considered unsuccessful if the coalition failed to gain tenure with a pride for the duration of the study period.

Demographic analysis

We recorded all nomadic and resident male coalitions observed within the study area from 1974-2012. Nomadic male sightings were opportunistic, as systematic search

effort targeted study area prides. Thus, we defined "search effort" using the GPS data of all the monthly sightings, pooled to 1-km^2 grid cells. We estimated minimum convex polygons for each month, assuming that the polygon area is independent of the number of individuals, and represents the search effort for a given month. Annual search efforts are estimated as the sum of monthly search efforts. We used general linear models to examine factors affecting nomadic males entering the study area, cub survival, and nomadic coalitions' success in gaining tenure. We used Akaike's information criterion (AIC) for model comparison and identification of the most parsimonious model (Zuur et al., 2009). All analyses were performed with Program R (R Core Team 2015).

Nomadic males entering the study area

We used general linear models to examine factors affecting the number of nomad coalitions entering the study area (nomad immigration), including as explanatory factors the year of immigration, the Southern Oscillation Index (SOI) in the year of immigration, and SOI in the year prior to immigration. Owing to year-to-year variations in the number of vehicles and research staff, we controlled for variability in nomadic lion monitoring by dividing our response variable (nomad immigration) by search effort each year. Note that all other demographic/population variables in this analysis were insensitive to search effort. To model nomad immigration, we used the 'CPLM' package in R and specified a Poisson distribution for continuous data with exact zeros (Zhang, 2013, 2015).

Nomad immigration, pride takeovers, and cub survival

We recorded the total number of cubs recruited to each pride in the study area, the proportion of cubs that survived to one year of age, the proportion of cubs that survived to two years of age, and the annual rate of pride takeover between 1974 and 2012. We

used general linear regressions to test whether the number of immigrating coalitions significantly affected the proportion of cubs surviving to one year of age, the proportion of cubs surviving to two years of age, and the annual rate of pride take overs. The models specified a Gaussian distribution and identity-link function (Zuur et al., 2009).

Coalitions gaining tenure with study prides

We examined factors affecting nomadic coalitions' success in gaining tenure with a resident pride in the study area, including as explanatory factors the immigration year, SOI during the immigration year and the year prior to immigration, the number of entering nomadic coalitions, resident prides, adult population size, median age of the nomad coalition in the year of entry, nomadic coalition size / average resident coalition size in year of immigration (relative coalition size), and the absolute size of the coalition. Relative and absolute coalition sizes were collinear and were modeled separately. Number of prides, population size, and immigration year were also collinear and modeled separately. Data were analyzed using generalized linear models with binomial distribution and logit-link function to account for the proportional nature of the data.

Results

Nomadic males entering the study area

From 1974-2012 a total of 471 coalitions (796 males) entered the study area, with a median annual immigration rate of 12.4 coalitions (Fig. 2a). Of these, 35 coalitions included males born into the study that were absent for a minimum of two years and then returned. The best model of nomad immigration included the explanatory factors: immigration year and SOI in the year prior to immigration. SOI in the previous year

reduced immigration in the current year (Table 1). The number of incoming nomadic coalitions was significantly and negatively correlated with year (Table 1). Notably, only a single nomad entered in 2008 (Fig. 2a). Conversely, the study population increased through time: the number of adults and prides in the study area were both positively correlated with year (Table 1).

Nomad immigration, pride takeovers, and cub survival

We recorded a total of 381 pride takeovers with a median annual rate of 10 takeovers. The number of coalitions entering the study area in a given year was significantly linked to the proportion of prides taken over in that year (Table 1): resident coalitions were significantly more likely to be ousted in years with large numbers of immigrating nomadic male coalitions (Fig. 2b).

The proportions of cubs surviving to one and two years were negatively affected by immigrating coalitions (Fig. 2c, Table 1).

Coalitions gaining tenure with study prides

From 1974-2012, 131 (28%) of the 471 incoming coalitions gained tenure with a study pride. The best model of coalitions tenure included: coalition age, coalition absolute size, and the number of nomadic coalition entering the study area (Table 1).

Success was significantly and positively related to coalition size. Successful incoming coalitions were larger than unsuccessful nomadic coalitions (Table 1, Fig. 3a), and this effect was relative: incoming coalitions were more likely to become resident when their coalition size was larger than the average resident coalitions in the population during that same year (Table 1, Fig. 3b).

The probability of nomadic coalitions gaining residency also increased with age (Table 1; Fig. 3c). The average age of successful incoming males was 5.46 ± 1.89 years vs. 4.23 ± 2.42 years for unsuccessful nomads (Fig. 4). Success rates of nomadic coalitions increased from ages two to six years as males reached their prime (Fig. 4).

Mating access was also density dependent with the number of nomadic coalitions affecting resident coalitions' ability to maintain tenure and each nomadic coalition's opportunity to gain pride tenure (Fig. 2b & 3d). The probability of individual nomadic coalitions gaining residency also decreased significantly with increasing numbers of incoming coalitions (Table 1; Fig. 3d). These dynamics affected cub survival across the entire study population (Fig. 2c).

Discussion

Males matter, especially in species where fathers must protect their offspring from the unkindness of strangers (Borrego et al., 2008; Rankin and Kokko, 2007). For lions, reproductive success depends on resident coalitions maintaining tenure long enough for their offspring to survive a subsequent takeover. Prides act as a limited resource that is essential to male reproduction, and inter-coalition competition produces a non-territorial population of nomadic males akin to 'floaters' in avian species (Penteriani et al., 2011). Accordingly, demographic factors affecting "competitive ability" successfully predicted whether nomads gained pride tenure.

Nomadic coalitions most often immigrated into the study area when the Southern Oscillation Index (SOI) was relatively weak and wet-season rainfall was heaviest, highlighting the potential role of environmental fluctuations on male dynamics,

particularly nomadic male dynamics. Variations in the SOI affect seasonal rains and vegetation abundance in the Serengeti (Sinclair et al., 2013), affecting the length of time migratory herbivores spend on the open plains (Packer et al., 2005). In years with positive SOI, resident lion populations benefit from increases in prey abundance (Ogutu et al., 2008; Sinclair et al., 2013), and the movement patterns of young dispersing males have been linked to annual rainfall (Elliot et al., 2014a; Funston et al., 2003; Packer et al., 1988; Pusey and Packer, 1987). During years with weak SOI, prolonged wet-season rainfall draws migratory wildebeest, zebra, and gazelle to the southeastern portion of the Serengeti ecosystem for extended periods (Packer et al., 2005). In turn, this continued presence of migratory prey may attract nomadic males from surrounding areas (Schaller, 1972).

A substantial proportion of incoming nomads originate from sub-populations that are exposed to trophy hunting, habitat loss, and retaliatory and ritualistic killing (Packer et al., 2009). Specifically, an increased demand for lion trophies has been linked to population declines in the areas bordering SNP (Packer et al., 2011; Packer et al., 2009). Although increasing anthropogenic pressures in surrounding areas likely explain the significant temporal decline in nomad immigration, the study population increased over the same period, and thus the protected SNP lions likely operate as a source to neighboring sinks. Compensatory hypotheses propose that reduced resource competition might 'compensate' for the loss of males from harvesting (Connell, 1978; Robinson et al., 2008), and indeed, the decline in males immigrating to our study population coincided with lowered takeovers, reduced infanticide, and greater cub survival in the study area.

However, compensatory growth cannot always be taken for granted (Cooley et al., 2009). Reduced infanticide might well have compensated for harvests of nomadic males during the years included in this study, but as human-wildlife conflicts intensify with the rapidly growing population in Africa, compensatory mechanisms may become overwhelmed. Following the illegal occupation of a substantial segment of Serengeti National Park by Maasai pastoralists, lions in the woodlands portion of the study area have declined since 2013 (CP, *unpublished data*). Coupled with the decline in immigrating nomads, the growing pressures in and around SNP threaten the future of this iconic lion population.

The removal of males from border regions may result in an initial boon to source populations, but if mortality is not balanced by increased reproduction and emigration, the resultant edge effect can cause the decline or extinction of core populations (Woodroffe and Ginsberg, 1998). Long-term declines in immigration can lead to inbreeding, population declines or crashes (Kissui and Packer, 2004). However, inbreeding alone is unlikely to cause complete population collapse and can be mitigated through relocation and outbreeding (Trinkel et al., 2008). Of greater concern is the risk from anthropogenic threats encroaching on protected areas and undermining an already fragile system. The compounded effects of ecological traps drawing breeding females out from the core (Pitman et al., 2015), edge effects from the preferential off take of males (Balme et al., 2010), and increased poaching within the source population may flip the wider system to a downward spiral (Pitman et al., 2015; van der Meer et al., 2014).

Implications for lion management

In open systems, like the Serengeti-Mara, lion population dynamics operate over large spatial and temporal scales. In the Serengeti, the movement of male lions regulates infanticide and is an important mechanism determining population stability. Thus, in these systems, conserving lions may depend not only on populations within protected areas but also on populations in regions bordering these areas. In contrast, closed systems prevent the immigration of infanticidal nomads, thereby removing natural checks on population growth and thus possibly leading to a problematic lion surplus (Miller et al., 2013; Miller and Funston, 2014). Lion populations throughout Africa are declining, with the general exception of lions in heavily managed, fenced reserves (Bauer et al., 2015; Packer et al., 2013). Wildlife managers in South Africa face a potential surplus of 90 lions per year in dozens of small populations that can sustainably hold a total of 700 individuals (Miller and Funston, 2014). Overpopulation in these small reserves has traditionally been resolved by translocating excess animals to new reserves, but this option is no longer feasible, and euthanasia is increasingly unacceptable to the general public. Alternatively, translocations of prime-aged males between pre-existing reserves could be treated as an experimental tool for testing whether males matter to lion population dynamics, even in their absence.

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Figure legends

Figure 1. Map of our study area (black dashed line) in Serengeti National Park and the surrounding areas. Trophy hunting is allowed in the Grumeti, Ikorongo, Maswa, and Loliondo areas. Pastoralist Maasai live in the Ngorongoro and Loliondo areas.

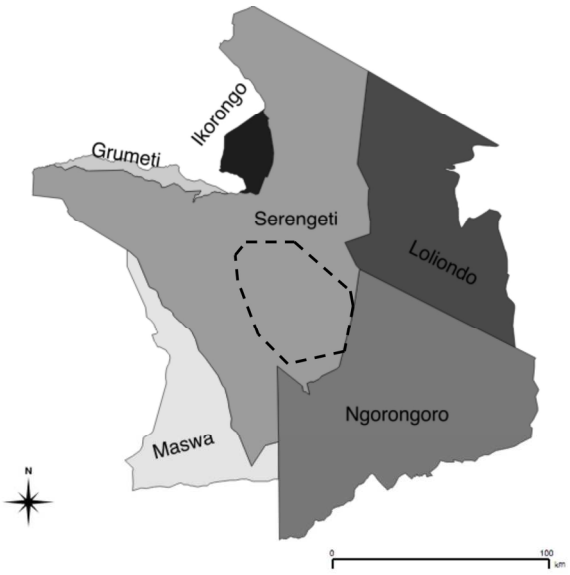
Figure 2. (a.) Yearly totals of nomad coalitions entering the study area, number of prides resident in the study area, and number of prides experiencing takeovers. Nomadic in-migrations declined through time while the number of resident prides increased. (b.) The proportion of study prides experiencing male takeovers was highest in years with the most incoming nomad coalitions. (c.) The proportion of cubs surviving to their first and second birthdays declined with increasing nomad immigration.

Figure 3. Factors affecting success rates of nomadic coalitions. The probability of a nomadic coalition gaining tenure with a study pride increased with increasing (a) absolute coalition size, (b) relative size, and (c) age and (d) decreased during years with greater numbers of immigrating coalitions.

Figure 4. The proportion of nomad coalitions in each age class that gained residence in a study pride.

Table 1. Summary of generalized linear models. The effect and standard error from the final model are reported for each term, and the effect of removing each term from the final model on the model Akaike's Information Criterion (ΔAIC).

Predictor	Effect	SE	p	ΔAIC
Number of immigrating nomad coalitions				
Immigration year	-0.07	0.008	**<0.0001****	40
SOI previous year	-0.03	0.01	**0.03***	2
Population size				
Year	0.01	0.002	**6.17E-06****	20
Pride takeovers				
Immigrating nomads	0.007	0.003	**0.04***	3
Number of prides				
Year	0.4	0.04	**7.93E-11****	43
Cub survival to one year				
Immigrating nomads	-0.006	0.003	**0.03***	-3
Cub survival to two years				
Immigrating nomads	-0.006	0.002	**0.02***	-3
Pride tenure				
Coalition absolute size	0.84	0.13	**<0.0001****	46
Coalition relative size	1.65	0.26	**<0.0001****	40
Coalition age	0.0001	0.0001	**<0.0001****	32
Immigrating coalitions	-0.04	0.01	**0.003****	7



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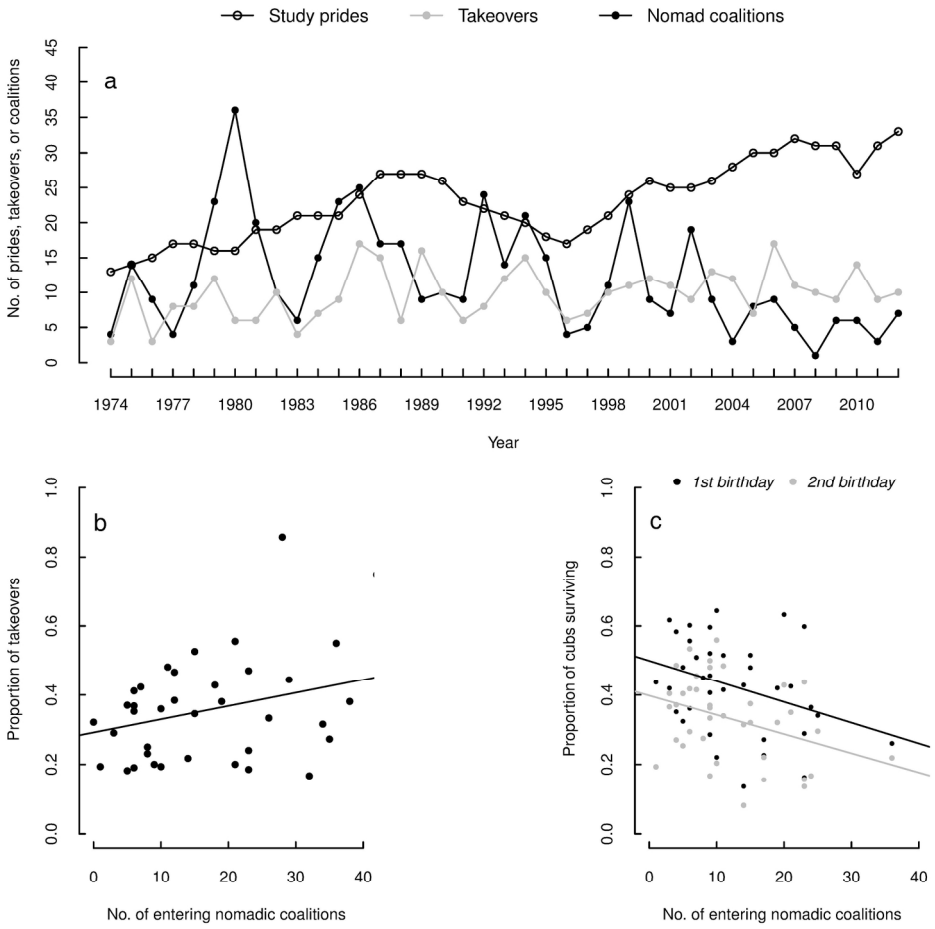

Figure 2. (a.) Yearly totals of nomad coalitions entering the study area, number of prides resident in the study area, and number of prides experiencing takeovers. Nomadic in-migrations declined through time while the number of resident prides increased. (b.) The proportion of study prides experiencing male takeovers was highest in years with the most incoming nomad coalitions. (c.) The proportion of cubs surviving to their first and second birthdays declined with increasing nomad immigration.

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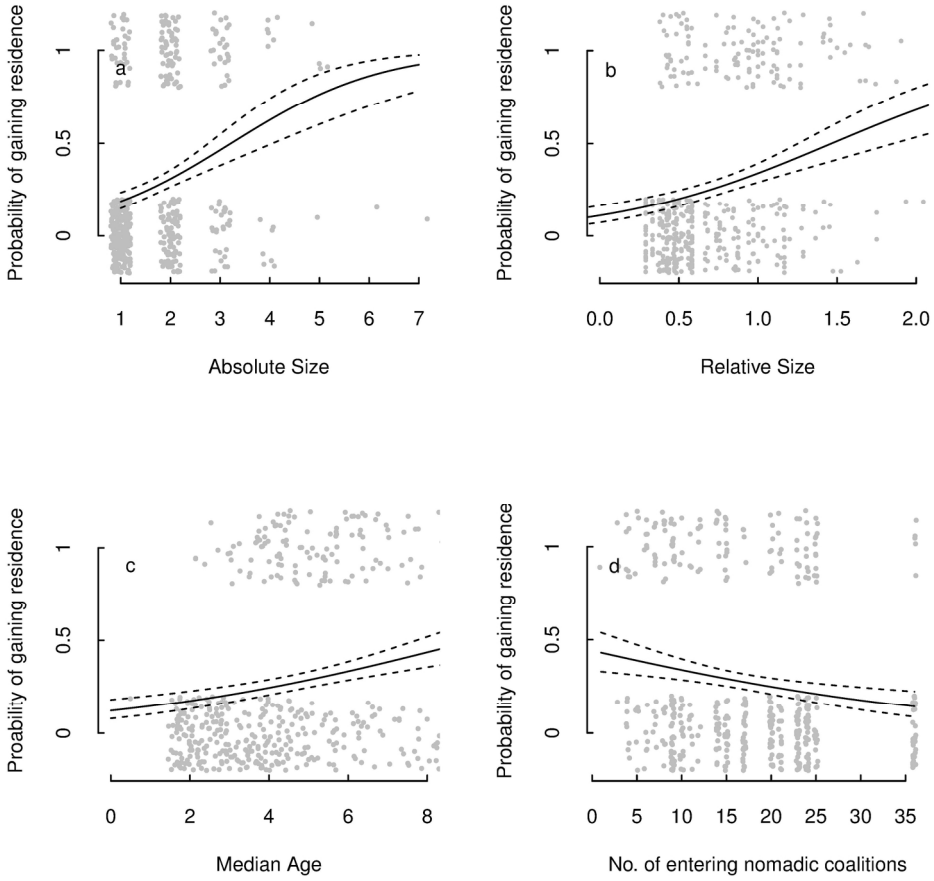

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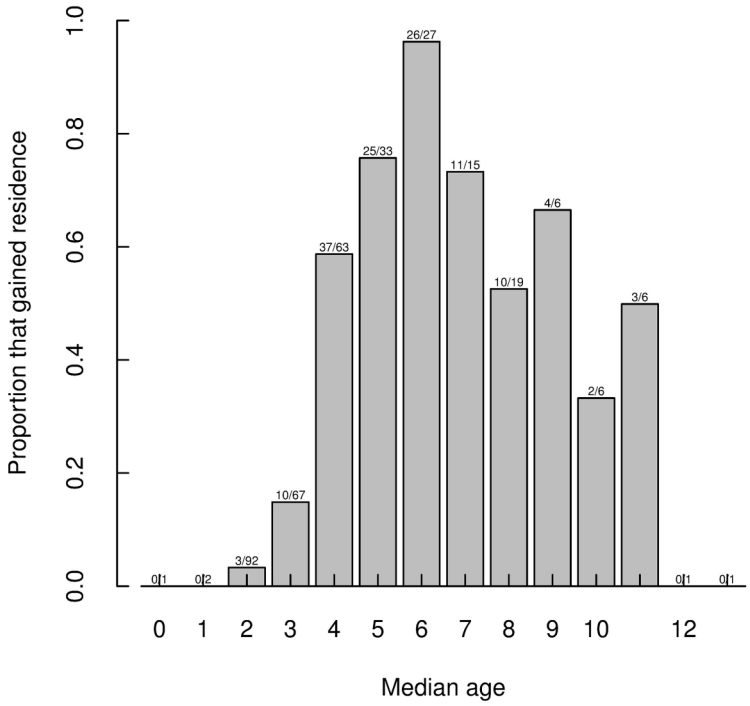

Figure 4. The proportion of nomad coalitions in each age class that gained residence in a study pride.

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